Gause, Luckinbill, Veilleux, and *What to Do*

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Alternative Models of Predation:

Functional Responses:

$$f\,(\mathrm{N}) \longleftrightarrow f\,(\mathrm{N/P})$$

"Prey Dependent"

"Ratio Dependent"

Possible Outcomes of a Predator-Prey System:

1) Complete consumption of prey followed by starvation of the predator ("**Dual Extinction**").
2) Oscillatory or non-oscillatory coexistence of predator and prey ("**Coexistence**")
3) Starvation of the predator followed by 'escape' of the prey ("**Predator Extinction**").

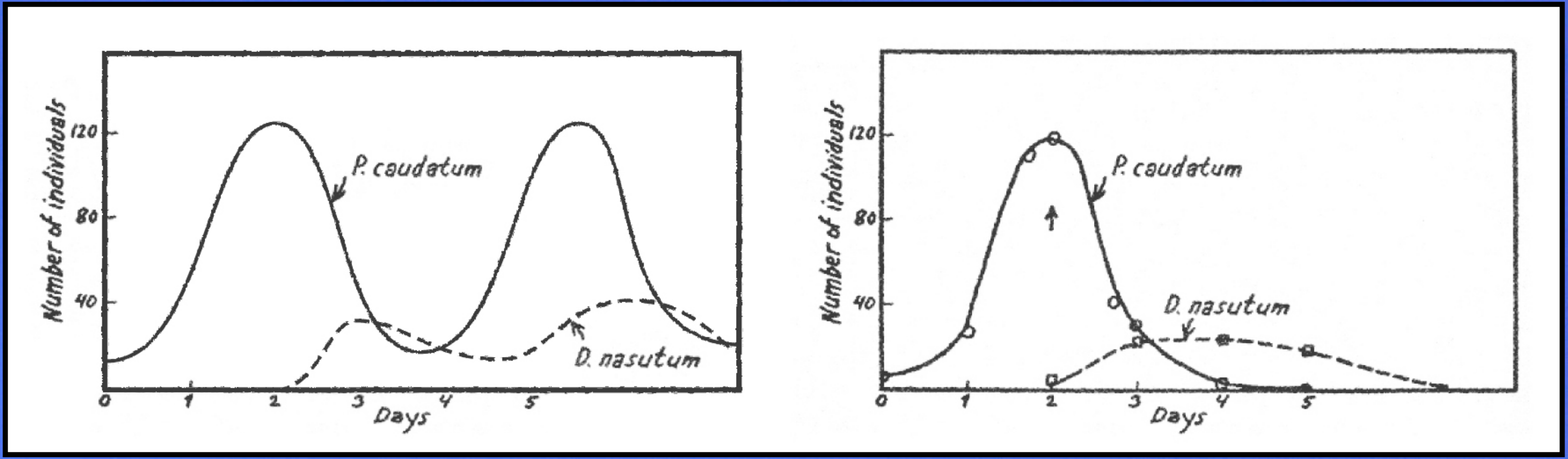
The *Paramecium-Didinium* system:

Paramecium caudatum

Didinium nasutum

Meets major assumptions of simple predator-prey models:
- Closed system
- Can be maintained without heterogeneities/refugia
- Single prey/single obligate predator
- Prey food can be delivered as semi-continuous input

Gause 1934:



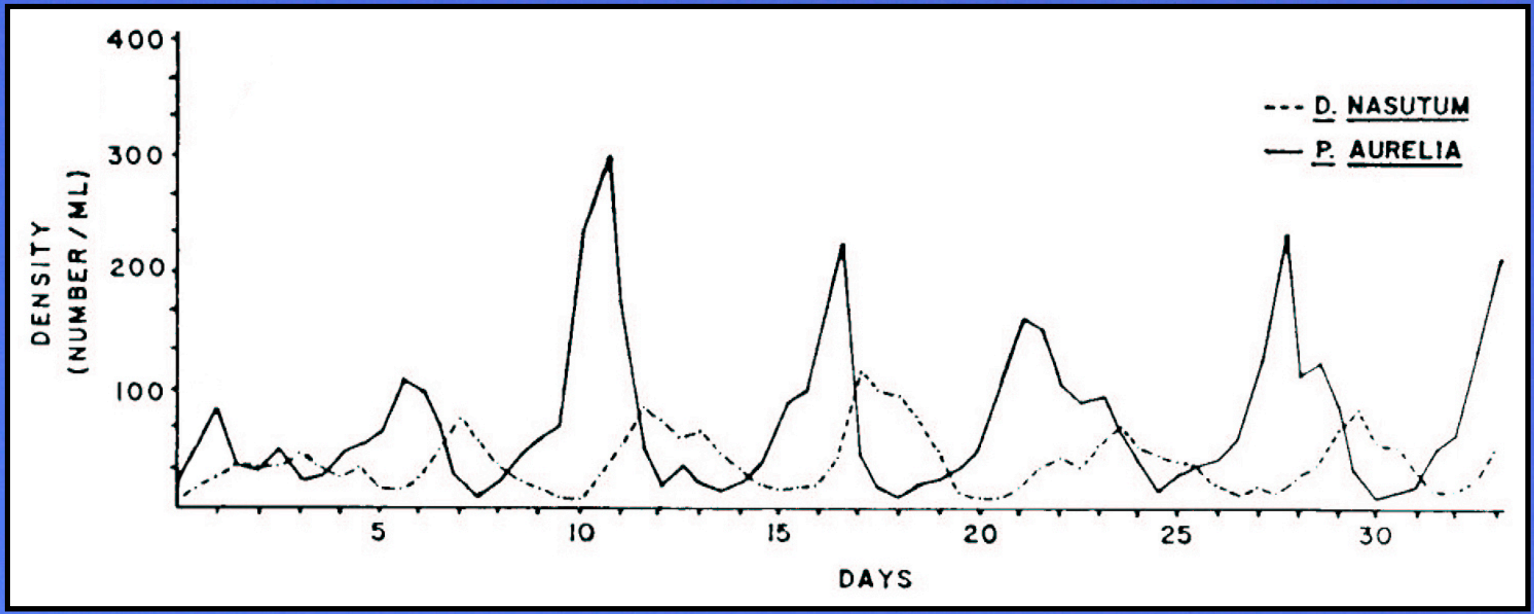
Expected:

Lotka-Volterra theory predicted that all predator-prey systems should cycle indefinitely

Actual:

Gause found that he could not prevent his predators from completely consuming the prey population

Luckinbill 1973:



Coexistence can be produced under two conditions:

1. Reduced interaction between predator and prey
2. Reduced prey food availability

Veilleux 1979:

Parameter Changes			Food Concentration	Number of Runs	System Outcome
High ***r***	high ***a***	high ***e***	1.80	17	Dual Extinction
↓	↓	↓	1.58	9	Dual Extinction (6x) and Predator Extinction (3x)
			1.35	18	Predator Extinction
			0.68 to 1.13	50	Coexistence
Low ***r***	low ***a***	low ***e***	0.18 to 0.45	20	Predator Extinction

Qualitative outcome can be changed through modifications of prey food concentration

What about fitting?

Prey-Dependence: better approximates Luckinbill 1973 data

Ratio-Dependence: better approximates Veilleux 1979 data

"Despite their structural difference, the two models can produce very similar temporal dynamics… both models fit very well to the data created by the other model. A good fit alone is therefore a poor indicator whether the used model correctly describes the processes that generated the data."

(Jost 1998, Jost and Ellner 2000, Jost and Arditi 2001)

What about fitting?

"Given that in real life there would be substantial variation around the respective functions, because of stochastic environmental effects, population censusing errors, and variation in parameters among different ecosystems, we submit that the subtle difference in predictions of the prey- versus ratio-dependent models is minor and would not be detectable using simple regression tests"

(Lundberg and Fryxell 1995)

Possible Outcomes of a Predator-Prey System:

1) **Dual Extinction**
2) **Coexistence**
3) **Predator Extinction**

Comparison of prey- vs. ratio dependent outcomes:

Change in Parameter	Prey-Dependent Outcome	Ratio-Dependent Outcome
a ↓ (searching efficiency)	DE → CoEx → PE	DE → PE; or DE → CoEx
K ↓ (carrying capacity)	DE → CoEx → PE	***no change***
r ↓ (prey growth rate)	***no change****	CoEx → DE
d ↓ (pred. death rate)	PE → CoEx → DE	PE → CoEx → DE
e ↓ (conversion eff.)	DE → CoEx → PE	DE → CoEx → PE
h ↓ (handling time)	PE → CoEx → DE	PE → CoEx → DE

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Proportional removal of prey will decrease *r* & *K* without changing other parameters:

$$dN/dt = r_0 N\,(1 - N/K) - pN$$

$$r_p = (r_0 - p)$$

$$K_p = K(1 - p/r_0)$$

Comparison of prey- vs. ratio dependent outcomes:

Change in Parameter	Prey-Dependent Outcome	Ratio-Dependent Outcome
$a\downarrow$ (searching efficiency)	DE → CoEx → PE	DE → PE; or DE → CoEx
Increasing levels of enforced proportional mortality (p)	DE → CoEx → PE	CoEx → DE
$d\downarrow$ (pred. death rate)	PE → CoEx → DE	PE → CoEx → DE
$e\downarrow$ (conversion eff.)	DE → CoEx → PE	DE → CoEx → PE
$h\downarrow$ (handling time)	PE → CoEx → DE	PE → CoEx → DE

Experiment: ***PoE in reverse***

H_P = increasing ***p*** (*i.e.* reducing ***K***) in a stable system should **maintain stability**.

[prey-dependent prediction]

H_R = increasing ***p*** (*i.e.* reducing ***r***) in a stable system should **destabilize the system**.

[ratio-dependent prediction]

Experiment: ***PoE forward***

H_R = decreasing ***p*** (*i.e.* increasing ***r***) in a stable system should **maintain stability**.

[ratio-dependent prediction]

H_P = decreasing ***p*** (*i.e.* increasing ***K***) in a stable system should **destabilize the system**.

[prey-dependent prediction]

Acknowledgements:

All of the thoughts presented are the result of extensive collaboration with Lev Ginzburg

I am fortunate to be supported by a *National Science Foundation* Graduate Research Fellowship and the L.B. Slobodkin Endowment Fund for Graduate Research.

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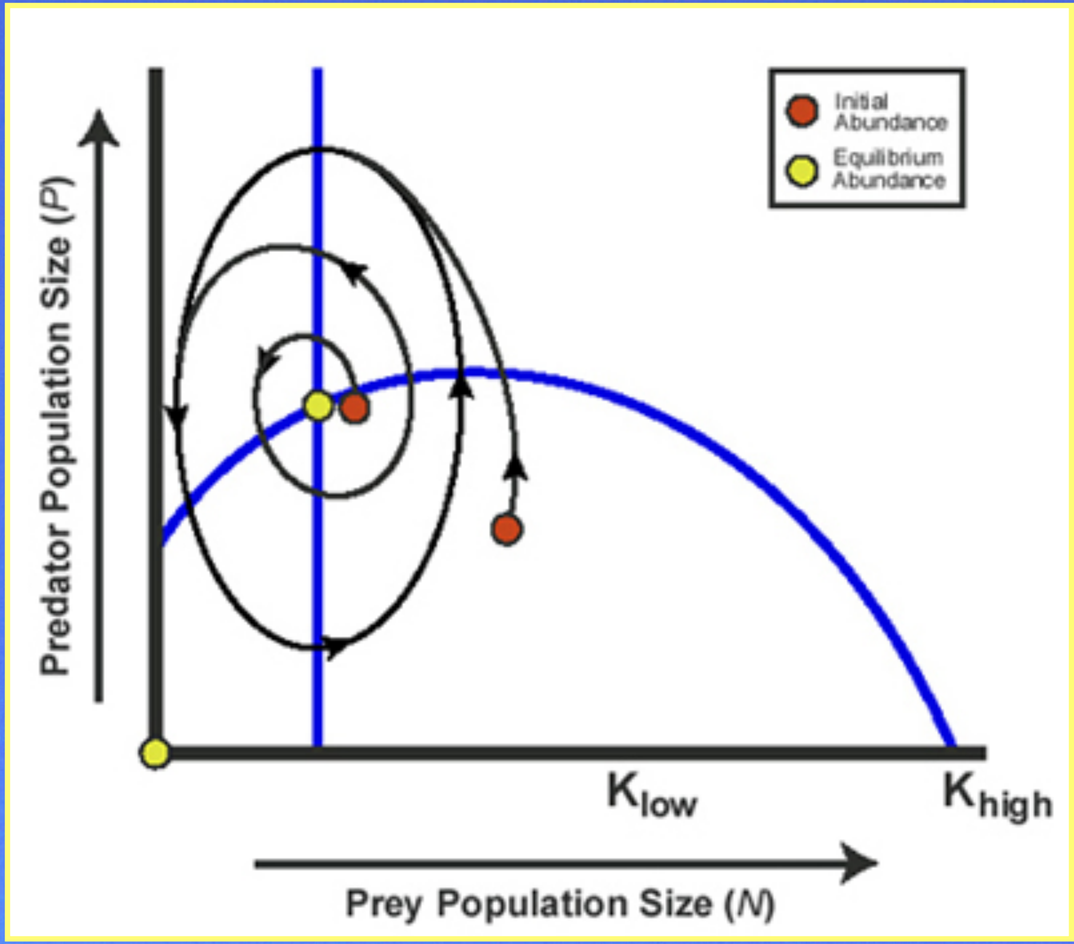
Experiment: ***PoE in reverse***

1. Using manipulations of methyl cellulose and prey nutrient input, find conditions under which long-term coexistence occurs
2. Impose proportional mortality of prey in as continuous a manner as possible
3. Continue to increase proportional mortality until *dual extinction* can be achieved
4. If dual extinction occurs, use a prey-only system with the same conditions to determine if the proportional mortality level at which *dual extinction* occurs corresponds to $r < 0$ or $r > 0$

Experiment: ***PoE forward***

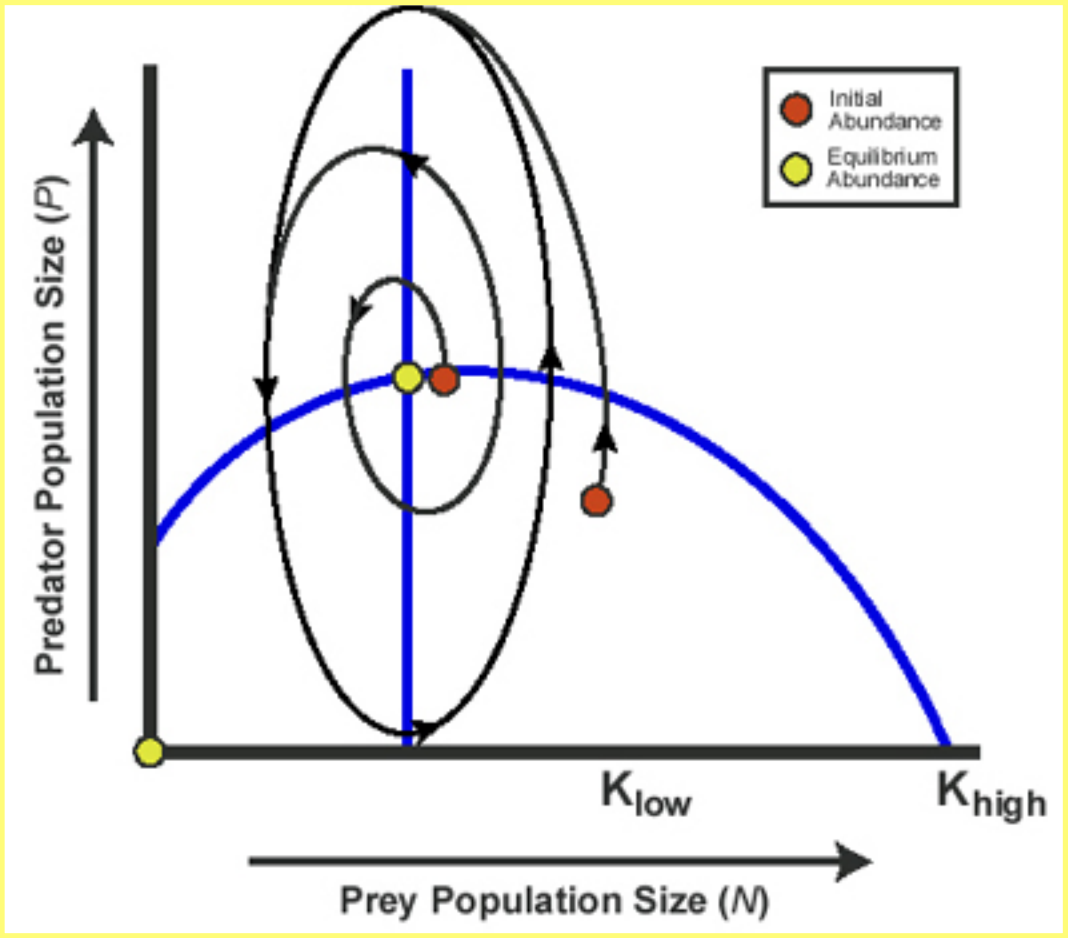
1. Begin with a system where high proportional mortality is being enforced
2. Using manipulations of methyl cellulose and prey nutrient input, find conditions under which long-term coexistence occurs
3. Increase *r* by incrementally releasing the system from enforced proportional mortality
4. Continue to decrease proportional mortality until *dual extinction* can be achieved
5. Note the problem here with having to prove the absence of a phenomenon

Luckinbill 1973:



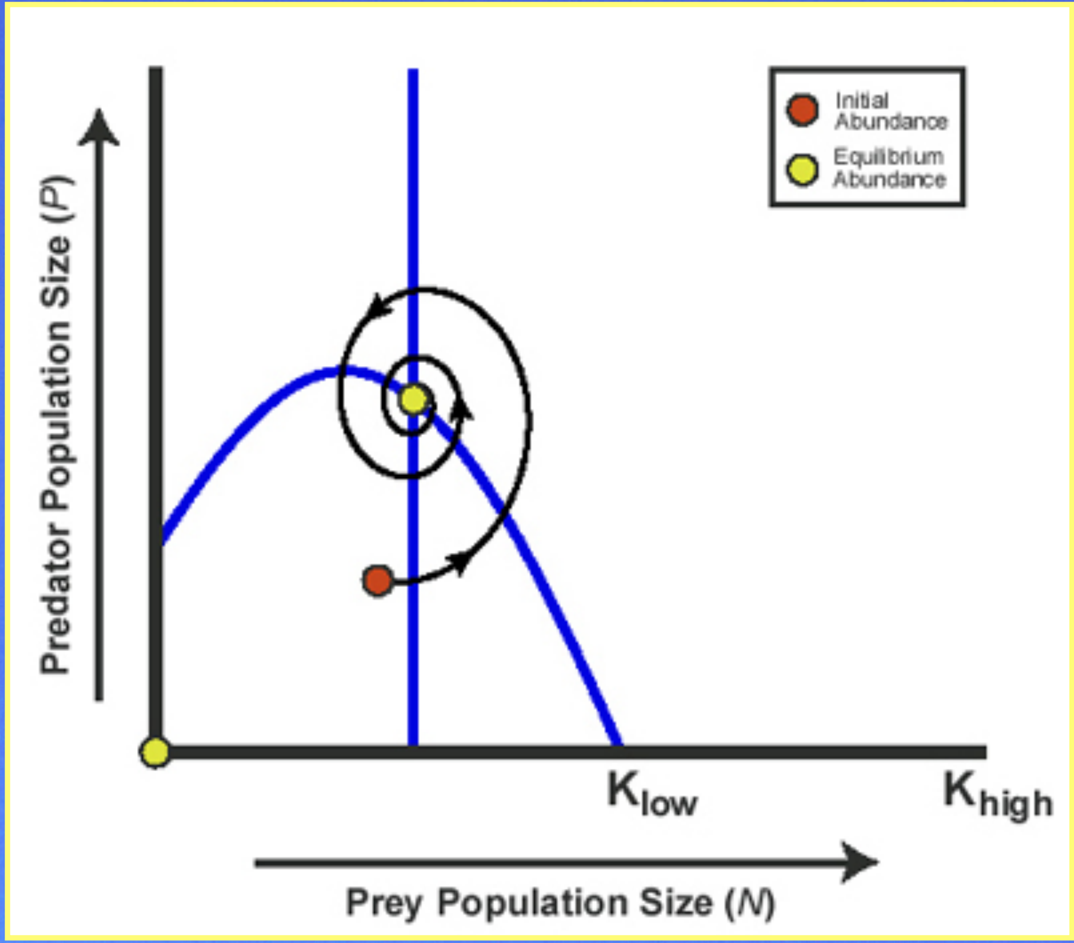
Dual Extinction

Luckinbill 1973:



Predator Extinction

Luckinbill 1973:



Coexistence